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UNDERWATER ORIENTATION IN THE SAND FIDDLER CRAB, *UCA PUGILATOR*

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The sand fiddler crab (*Uca pugilator*) inhabits the intertidal and supratidal zones of sheltered sandy coastlines from Cape Cod to Texas (Crane, 1943). As with other ocypodids, its semi-terrestrial designation stems from its physiological dependence upon periodic submersion and from its behavioral activity on aerially-exposed substrates. Burrows dug in the sand serve as shelter during predatory attacks and high tides, as immediate sources of water, and as focal points of social activity. Occasionally, a crab is forced to seek refuge in the water when access to the burrows is blocked by pursuing predators such as plovers, willets, raccoons, clapper rails, etc. (Herrnkind, 1972; Teal, 1958; and personal observation). It then becomes vulnerable to attack by such aquatic predators as fish and the portunid crabs, *Callinectes sapidus* and *Carcinus maenas*. Hence, it would be of selective advantage for *Uca pugilator* to possess some means of detecting the direction of the shore and a suitable burrow while submerged. Indeed, field releases of free-ranging *U. pugilator* in shallow offshore waters result in marked orientational movements toward shore (L. M. Lutton and D. Y. Young, unpublished data; W. F. Hernkind, unpublished data).

Terrestrial orientation in the genus *Uca* has been investigated only in recent years (Altevogt, 1965; Altevogt and von Hagen, 1964; Herrnkind, 1966, 1967, 1968, 1972). A thorough review of orientation in shore-inhabiting arthropods, with specific reference to *Uca pugilator*, is given by Herrnkind (1972). On aerially exposed beaches *U. pugilator* utilizes a time-compensated sun compass, supplemented by telotactic responses to landmarks for directed movements of distances greater than one meter ("far orientation"). Kinesthesia of substrate features is not known to influence orientation over these distances. Instead, kinesthetic cues are said to be limited to above water movements of less than one meter ("near orientation") (Herrnkind, 1972).

Orientation cues available to the crab underwater potentially differ from those on land due to differences in the physical characteristics (*e.g.*, refractive index, specific gravity, transparency, etc.) between sea water and air. Visual cues, such as those emanating from celestial and landmark sources, may be available to submerged crabs as well as to those situated on the exposed portions of the beach. Celestial cues involve the sun's position and/or polarized light. Landmarks could be detected as differential light intensities created by beach grasses, trees, and mangroves set against a sky or sand background. In both cases, the apparent

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position of the cues is refractively modified by the air-water interface. These cues are also subject to distortion by variable water surface conditions. Sea water, having a specific gravity and light absorptive index greater than those of air, may also allow submerged crabs to use some gradient cues for shoreward orientation. Any vertical movement in water will result in greater changes in ambient pressure and light intensity than those ensuing from an equal movement in air. Theoretically, movements along a decreasing pressure gradient would eventually allow a submerged crab to reach land, even in the absence of celestial and landmark cues. Appropriate movements along gradients of light intensity and or light wavelength will similarly result in the crab's leaving the water. Likewise, upward movements along substrate slopes will generally lead out of the water.

Many animal orientation systems entail redundant schemes of cues in which certain stimuli, or combinations thereof, dominate others in a hierarchial or synergistic fashion (Adler and Taylor, 1973; Bellrose, 1965; Ferguson, 1965; Keeton, 1971; Papi and Pardi, 1953; Papi and Tongiorgi, 1963; Williamson, 1951). In this paper we attempt to ascertain the cues that are utilized in underwater orientation by *Uca pugilator* and any hierarchial arrangement of these cues.

Materials and Methods

Most of the experiments were conducted at Orient Beach State Park, Long Island, New York, during July, August, and September, 1972, and the Mote Marine Laboratory, Placida, Florida, in January, February, and March, 1973. Four experiments were performed with Florida crabs at Ithaca, New York.

The crabs were tested in two tall narrow tanks made of clear 0.6 cm levate (Plexiglas); the interior dimensions were 77.6 cm long, 12.5 cm wide, and 51.5 cm high. Since the focus of this study was only upon whether the crabs oriented landward or seaward, the absolute compass bearing of the released crabs was inconsequential. Accordingly, the narrow or "one-dimensional" characteristic of the testing tanks provided the subjects with essentially only two directions in which to travel. An open-topped rectangular tank served as the standard testing apparatus, and a trapezoidal tank was used in the gradient experiments to be discussed later.

At the bottom of each testing tank was a levate ramp, with an adjustable angle of inclination, in which 3 mm wide "foothold" grooves had been cut. Test crabs were introduced from above through a 2.5 cm ID (internal diameter) levate tube, 63 cm in length. The experimenter, standing 6 m away on a line perpendicularly bisecting the long axis of the tank, could release a crab by removing a wire platform located beneath the crab and 10 cm from the top of the tube. A small lead sinker above the crab forced the crab onto the middle of five contiguous, congruent zones (each 15.2 $\times$ 12.1 cm) marked on the ramp.

Generally, the testing apparatus was submerged in 20 to 30 cm of water directly offshore and perpendicular to the crabs' home beach. The home burrows were within 15 m of the tank. The water level inside the tank was maintained within 4 cm of that of the surrounding water. To minimize the possible accumulation of metabolites within the tank, the water was changed after every 6 to 7 crab releases using local sea water. Since above-water orientational responses vary

TABLE I

Experimental results of control and isolated cue experiments, comparing the number of crabs orienting in one direction against the number orienting in the opposite direction. Asterisks denote significance at the 0.05 level. Approximate times of day are given for those tests involving celestial cues.

Experiment	Location	Month	Approx. time	Number of crabs orienting toward:		Significance level (two-tailed)
				Home beach	Deep water	
Control I "natural" conditions	Florida	Jan. 73	1500–1700	16	1	$P < 0.001$*
		Feb. 73	1130–1300	15	0	$P < 0.001$*
		Mar. 73	1430–1615	17	0	$P < 0.001$*
	Long Island	Jul. 72	1645–1845	17	2	$P < 0.005$*
		Sep. 72	1430–1730	22	10	$P > 0.05$
Control II total overcast	Florida	Jan. 73		10	9	$P > 0.95$
landmarks obscured tank level	Long Island	Aug. 72		10	9	$P > 0.95$
Celestial cues only	Florida	Jan. 73	1330–1700	15	1	$P < 0.005$*
	Long Island	Aug. 72	1230–1445	14	4	$P < 0.05$
Landmark cues only	Florida	Jan. 73		20	4	$P < 0.005$*
	Long Island	Aug. 72		17	13	$P > 0.5$
Gradient cues only	Florida	Feb. 73		20	9	$P > 0.05$
		Aug. 73		15	5	$P < 0.05$*
		Aug. 73		18	7	$P < 0.05$*

among crabs of different size and age categories (Herrnkind, 1972), only typically colored male and female adults with carapace width greater than 10 mm were used. They were captured and tested one at a time during daylight hours of normal feeding and/or social activity. Once captured, the test crab was transported in a closed fist along the straightest line to the experimental tank. After a crab was released, the time it spent in each zone was recorded and its position noted after two minutes. Each individual was tested only once, marked, and then returned to the capture site. Marked crabs were not used in subsequent tests.

The following experimental manipulations were executed in order to determine the factors involved in landward orientation.

Controls

Control I. To ensure that crabs could orient landward while submerged in the testing tank, experiments were periodically conducted under "natural" conditions. The skies were clear and sunny, beach landmarks were available, and the testing tank was placed in the water on the natural slope of the subtidal and intertidal zones. The dates of the experiments are presented in Table I.

Control II. If the crabs could orient in the absence of celestial, landmark, and gradient cues, then they would have to be utilizing some aspect of the environment that we had not yet considered. Experiments to test this hypothesis were performed on heavily overcast days when sun and blue skies were not visible to human observers. The testing tank was levelled on the substrate in order to eliminate possible gradient cues. Landmarks were obscured by surrounding the tank with a screen constructed of four layers of translucent polyethylene sheeting (0.02 cm in thickness) stretched around eight poles. The resulting octagonal arena measured 0.97 m high and approximately 2.5 m in diameter.

Isolation of cue systems

Each of the three cue systems was isolated by eliminating the other two in the following manner.

Celestial cues. Experiments were conducted under clear, sunny skies with the tank levelled and the landmark-obscuring screen in place.

Landmark cues. The tank was levelled and the experiments were performed on days of total overcast.

Gradient cues. The tank was set on the natural slope of their home shore (3°–5°) with the landmarks obscured and the skies totally overcast. The infrequency of overcast days in southwestern Florida, however, forced collection of a large majority of these data under modified conditions. The testing tank was submerged in a circular plastic wading pool, 1 m in diameter, located in a radially symmetrical tent lined with black plastic to eliminate celestial and landmark cues. A 9° inclination was created *via* the adjustable ramp. The crabs could not be collected and tested individually since it was not possible to place the tank, pool, and tent within reasonable distance of their burrows. Consequently, they were collected in lots of eight to ten, transported in a light-proof container, and tested within 90 minutes of capture.

Conflict of cue systems

Pairs of cues that both normally indicated the direction of the home beach and that were shown to be used by crabs were conflicted to give opposing directional information. The resultant behavior in this conflict situation was assumed to be indicative of the dominance (if any) of one stimulus over the other. Pairs of different cue systems were conflicted as follows.

Gradient cues vs. celestial cues. Crabs were tested with the sun shining brightly, the landmarks obscured, and the gradients reversed. In other words, the deeper end of the tank was closest to the home beach. Subjects that moved toward deeper water would be orienting according to celestial cues, and thus reveal that celestial cues dominate gradient cues. Crabs that oriented toward the shallow end of the tank would indicate preferences for gradient cues over celestial cues.

Landmark cues vs. celestial cues. In order to conflict landmark and celestial cues, the entire experimental apparatus was transported 0.7 km to an opposing but parallel beach on a small "spoil" island on the west side of the Intra-Coastal Waterway. The short pines, mangroves, and beach grasses of this beach resembled the vegetation of the home beach. Twenty crabs were collected on the home beach, transported in lightproof containers to the opposing beach, and tested individually within 75 minutes of capture.

Gradient cues vs. landmark cues. On a totally overcast day, gradient cues were conflicted with landmark cues by sloping the tank upward, away from the landmarks on the home beach.

Gradient cues

The gradient cue most obvious to a crab on the shore is presumably the substrate slope; underwater movements, however, could involve gradients of light intensity, light wavelength, and pressure, as well as the substrate slope. Temperature and chemical gradients were not likely to exist in the region of shore that we were considering due to constant mixing. Once it was established that, in fact, the crabs did respond to gradient cues in the absence of landmark and celestial cues, the next problem was to determine which gradient cues were utilized and how they were related.

For this series of experiments, a tank with a floor similar to the rectangular tank but with trapezoidal sides, was constructed of 6 mm clear levate. A sagittal view of this tank resembled a right triangle that was truncated and opened at its upper acute corner. During all of the following experiments, this tank was levelled and submerged in 10 cm of water in the wading pool within the tent. The crabs were collected in lots of ten, held in a lightproof container, and tested individually within 90 minutes of capture. The August, 1973 experiments were conducted in Ithaca, New York, with crabs from Clearwater, Florida. They were transported by car and testing began within 48 hours of capture. While in Ithaca, the crabs were "housed" on artificial beaches under the same tidal regime and photoperiod as those of their home beach.

Light intensity and light wavelength. All vertical surfaces of the tank were covered with black polyethylene, permitting light to reach the bottom of the tank only through the slanted top surface. Two fluorescent bulbs [producing 75 footcandles (1.19 watts m^2) at one foot and having a correlated color temperature of 4300° and a color rendering index of 69] were positioned 1.2 m above and parallel to the tank bottom. While these lamps may not accurately mimic sunlight, light intensity and light wavelength gradients were nevertheless established along the tank bottom in the absence of any substrate slope or changing water pressure. The hydrostatic pressure at every point along the tank bottom was equal to the highest column of water (51 cm). Each crab was released into the central region of the light gradient by means of an introduction tube, like that used in the rectangular tank. A crab travelling toward the "short" end of the tank encountered photic conditions resembling those met during movements from deep water to shallow water. The covered sides of the tank created a problem; once a crab was released, its movements could not be monitored without disturbing the crab or destroying the light gradient. Consequently, for 2 minutes after it was released, the test subject was left undisturbed. At the end of that period the experimenter peered over the top of the tank and noted the crab's position along the bottom. Any movement after that point might have been a fright response and was not included in the analysis.

Hydrostatic pressure. Creating a hydrostatic pressure gradient while maintaining a level substrate proved to be impossible. However, by servoing the pressure at the tank bottom to the position of the crab, a pressure gradient could be simulated while eliminating gravitational and photic cues. As the crab moved toward one end of the tank, the pressure within the tank was gradually increased; if it moved in the opposite direction the pressure was correspondingly decreased.

The trapezoidal tank was modified for this pressure gradient experiment. An opaque gasket-lined cover was fitted onto the opening at the "tall" end of the tank. Leading through this cover was 15 cm of flexible 1.9 cm ID tubing. A "pressure tube" of rigid Plexiglas (63 cm long, 2.5 cm ID) was connected to the distal end of the flexible tubing. To eliminate light cues all tank surfaces, with one exception, were covered with black polyethylene. The lower 8 cm along one side was left open to light to enable the experimenter to monitor the test subject's position and adjust the pressure accordingly. The maintenance of positive pressure within the tank necessitated the sealing of the crab introduction tube. Each trial began by placing the crab in the tube on a hinged metal platform that remained horizontal as long as a magnet was placed on the outside of the tube. The introduction tube was then filled with sea water and sealed with a rubber stopper. Next, the pressure tube was held at an angle of approximately 3° above horizontal, filled with sea water, and left open to the air. As this tube was raised to a vertical position the height of the column of water within the tube rose, gradually increasing the pressure within the tank. The maximum pressure change that could be created at the tank bottom was equivalent to a simulated slope of 12°. With the pressure set midway between the maximum and minimum levels, the magnet was removed from the outside of the introduction tube, and the test crab dropped down to the tank bottom. The hydrostatic pressure within the tank was then manually servoed to the movements of the crab for two minutes, using the full range of pressure (53–69 cm of water).

Light intensity, light wavelength, and pressure. Only minor changes in the pressure gradient set-up were required in order to create a combination of light intensity, light wavelength, and pressure gradients in the absence of substrate slope. First, the black plastic covering the top slated surface of the trapezoidal tank was removed to supply the light gradients. Next, to prevent light from entering the window through which the crab's movements were monitored, an "awning" of black cardboard was erected above the observation window. Each crab was then tested in the same fashion as described in the pressure gradient experiment.

The analysis of the data from the Long Island and Florida crabs was divided into three phases. First, in each experiment dealing with different cues regimes, the number of crabs orienting in one direction was compared to the number orienting in the opposite direction. Next, the proportions of shoreward orienting crabs from different experiments were compared. Finally, the times required for orientation in the different experiments were compared. Each crab's orientation time was the number of seconds taken to finally enter the zone in which it remained until the end of the trial. Hence, a crab that wandered continuously would have an orientation time close to 120 seconds; an orientation time of 5 seconds would characterize a crab that headed toward one end of the tank upon release and remained in that end zone until the termination of the trial. Any crab found in the central three zones after two minutes was considered to have not oriented and was not considered in this analysis.

The numbers of crabs orienting in opposite directions within a given experiment were compared using a Chi-square test, corrected for continuity (Snedecor and Cochran, 1967). [These results are presented in Table I and Table II.]

Table II

Experimental results of conflicted cues and gradient aspects, comparing the number of crabs orienting in one direction against the number orienting in the opposite direction. Asterisks denote significance at the 0.05 level. Approximate times of day are given for those tests involving celestial cues.

Experiment	Location	Month	Approx. time	Number of crabs orienting according to:		Significance level (two-tailed)
				Gradients	Celestial cues	
Gradient *vs.* celestial cues	Florida	Jan. 73	1200–1515	5	17	$P<0.025$*
	Long Island	Aug. 72	1250–1500	5	12	$P>0.1$
				Landmarks	Celestial Cues	
Landmarks *vs.* celestial cues	Florida	Feb. 73	1300–1415	4	15	$P<0.025$*
				Gradients	Landmarks	
Gradient *vs.* landmarks	Florida	Mar. 73		7	10	$P>0.5$
				Number of crabs orienting toward:		
				Shallow water	Deep water	
Light intensity and light wavelength gradients	Florida	Mar. 73		8	12	$P>0.5$
Pressure gradient	Florida	Aug. 73		14	10	$P>0.5$
Light intensity, light wavelength and pressure gradients	Florida	Aug. 73		9	8	$P>0.9$

The proportions of shoreward orienting crabs from various experiments were compared using a 2 × 2 contingency table and either the Chi-square test, corrected for continuity, or the Fisher exact probability test, depending on the size of the sample (Siegel, 1956).

Results

Controls

Florida crabs consistently oriented toward their home beach under "natural" conditions when celestial, landmark, and gradient cues were available (Control I) (Table I). No temporal changes in the crabs' ability to orient toward shore were noted, since one experiment was performed at the beginning of the Florida series of experiments (January, 1973), one in the middle (February, 1973), and one at the end (March, 1973). The Long Island crabs also displayed orientation toward shore, but with more ambiguity than their southern counterparts. The results of the July experiment were highly significant ($P < 0.005$; Table I). The results of the September experiment yielded a nonsignificant χ^2 of 3.78 (χ^2 critical, $\alpha = 0.05$, with 1 d.f. $= 3.84$).

A comparison between the proportions of Long Island and Florida populations that oriented under "natural" conditions revealed that Florida crabs oriented toward shore more frequently than did Long Island crabs ($P < 0.05$; Table III).

TABLE III

Comparisons of the proportions of shoreward orienting crabs from pairs of selected experiments. Asterisks denote significance at the 0.05 level.

Experiment	Location	Number of crabs orienting toward:		Test	Significance level (one-tailed)
		Home beach	Deep water		
Control I	Florida Long Island	48 39	1 12	χ^2	$P < 0.005$*
Celestial only Landmarks only	Florida	15 20	1 4	χ^2	$P > 0.25$
Celestial only Gradients only	Florida	15 53	1 21	χ^2	$P < 0.05$*
Landmarks only Gradients only	Florida	20 53	4 21	χ^2	$P > 0.1$
Celestial only Gradients *vs.* celestial	Florida	15 17 (cel.)	1 5 (grad.)	Fisher	$P > 0.1$
Celestial only Landmarks *vs.* celestial	Florida	15 15 (cel.)	1 4 (land.)	Fisher	$P > 0.2$

When neither celestial, landmark, nor gradient cues were present (Control II) both Long Island and Florida crabs distributed themselves evenly toward and away from shore (Table I). Thus, it is unlikely that magnetic fields, or other visual cues influenced the orientation of the crabs under these test conditions. While the nature of the testing apparatus isolated the test crabs from the potential influence of wave surge and nearshore water currents, hydrodynamic cues are often absent in the shallow, protected estuaries characteristic of the habitat of *U. pugilator*.

Isolated cues

When only celestial cues were present, both the Florida and Long Island groups of crabs were able to direct themselves toward shore ($P < 0.005$ and $P < 0.05$, respectively). However, with only landmark cues available, the Florida crabs displayed significant shoreward orientation ($P < 0.005$), while the Long Island crabs did not ($P > 0.05$) (Table I).

Results of tests on three different groups of Florida crabs presented with only gradient cues are shown in Table I. Two of the three experiments resulted in significant landward orientation, while the remaining experiment yielded a non-significant χ^2 of 3.44 (χ^2 critical, $\alpha = 0.05$, with 1 d.f. = 3.84). Long Island crabs were not tested for their ability to use gradient cues alone due to the lack of appropriate facilities there.

The proportion of Florida crabs that oriented shoreward when only celestial cues were available was significantly greater than the proportion that used only gradient cues ($P < 0.05$). No such difference was apparent between celestial and landmark cues, nor between landmark and gradient cues (Table III).

Conflict of cue systems

When landmarks were eliminated and gradient cues were conflicted with celestial cues, there was no significant orientation among Long Island crabs that was consistent with either cue system. Among the Florida crabs, a significantly larger number oriented with the celestial cues than with the gradient cues ($P < 0.025$) (Table II). Nevertheless, there was no significant difference between the results of this gradients *vs.* celestial cues experiment and those of the isolated celestial cues experiment. In other words, the presence of the opposing gradient cues did not significantly affect the proportion of the crabs that normally respond to celestial cues alone (Table III).

The conflict between landmarks and celestial cues, in the absence of any gradient cues, results in a marked dominance of celestial cues ($P < 0.025$) (Table II). Again, the presence of opposing landmarks did not significantly affect the proportion of crabs that oriented according to celestial cues alone (Table III). The dominance of celestial cues over landmarks might be more convincing had the landmarks on the "spoil" island been shown to be effective guidance cues in the absence of gradient and celestial cues.

When gradients and landmarks were presented in opposing fashion, neither cue system displayed a clear dominance over the other (Table II).

Gradient cues

Having established that *Uca pugilator* is capable of using some gradient(s) for shoreward orientation (Table I), it was necessary to determine which aspect(s) of a water depth gradient the crabs were using. A combination gradient of light intensity and light wavelength did not result in any significant orientation of the crabs (Table II). Likewise, a simulated hydrostatic pressure gradient appeared to be an ineffective stimulus (Table II). When the crabs were subjected to a combined gradient of pressure, light intensity, and light wavelength no significant response resulted; approximately half the crabs travelled toward deep water and half toward shallow water (Table II). It is highly unlikely, however, that these crabs at this point had lost their ability to orient with gradient cues. As a test, at the next low tide another batch of crabs from the same beach was presented with all of the gradient cues; light intensity, light wavelength, hydrostatic pressure, and substrate slope. The outcome, previously presented, shows significant shoreward orientation (18 crabs oriented toward shallow water and 7 toward deep water) ($P < 0.05$) (Table I).

In all cases where significant orientation occurred under the same experimental conditions in both Florida and Long Island crabs, statistical comparisons of the orientation times between the two sites were made. Under "natural" conditions, it was found that Florida crabs ($\bar{X} = 21.0$ sec, $N = 44$) oriented sooner after release than Long Island crabs ($\bar{X} = 39.1$ sec, $N = 22$) ($P < 0.05$, Table IV). No significant difference existed between the orientation times of Florida and Long Island crabs when both groups were exposed only to celestial cues (Table IV).

Florida crabs that were presented with either isolated celestial cues, landmarks, or gradients did not significantly differ in their orientation times. For instance,

TABLE IV

Comparisons of the orientation times from selected experiments. Asterisks denote significance at the 0.05 level.

Experiment	Location	$\bar{X}$, sec	N	Test	Significance level (one-tailed)
Control I	Florida	21.0	44	Mann-Whitney U	$P < 0.05$*
	Long Island	39.1	22		
Celestial only	Florida	19.0	14	Mann-Whitney U	$P > 0.1$
	Long Island	30.9	11		
Celestial only	Florida	19.0	14		
Landmarks only	Florida	40.7	18	Kruskal-Wallis	$P > 0.1$
Gradients only	Florida	56.8	50		
Gradients *vs.* landmarks					
Gradients	Florida	48.5	4	Mann-Whitney U	$P > 0.1$
Landmarks		17.2	6		

celestial cues did not result in significantly faster orientation than either landmarks or gradients (Table IV).

DISCUSSION

The terrestrial orientation of *Uca pugilator* has been investigated by Herrnkind (1972). On aerially exposed substrates, landmarks and celestial cues, in the form of sun position and polarized light, are utilized for directional guidance. Celestial cues generally override landmark cues in cases where they conflict. Kinesthetic cues are used only in the immediate vicinity of the burrows. Among the species studied so far, gravitational cues act as guideposts in the wolf spider *Arctosa* (Herrnkind, 1972), the isopod *Tylos punctatus* (Hamner, Smyth, and Mulford, 1968), and the amphipod *Orchestroidea corniculata* (Craig, 1973).

Underwater orientation in *Uca pugilator* involves the use of gradient cues, as well as landmark and celestial cues. Each cue system alone would permit a crab to emerge from the water (Table I). While celestial cues appear to be more influential than landmark and gradient cues (Table II), the relative importance of the latter two cue systems is not as obvious. Neither proved to be the dominant mode when they were conflicted (Table II). It should be noted, however, that the one-dimensional character of the test tanks obscures any response having an angular component relative to the axis of the tank. When landmarks were conflicted with gradients, the time the crabs took to orient according to either system did not significantly differ (Table IV). It must be noted, though, that a type II error is quite likely in this case due to the small sample size ($n_1 = 4$, $n_2 = 6$). If the respective orientation times were different, perhaps a more subtle form of dominance was then occurring, such as rate of orientation.

Landmark cues take the form of differential light intensities along the horizon. Celestial cues are potentially available to the underwater crab in three forms: the sun's position, the polarized light of blue sky (as in the terrestrial case), and the polarized daylight originating from the water itself (Waterman, 1954). Since the latter two are ultimately dependent upon the sun's position, little is gained from attempts to conflict assorted pairs of the trio.

Gradient cues exist as light intensity, light wavelength, and hydrostatic pressure gradients, as well as substrate slope. The results here tend to reject the hypothesis that *Uca pugilator* employs any combination of the first three gradients for shoreward orientation. Barosensitivity among brachyurans is generally limited to the planktonic larval stage (Baylor and Smith, 1957; Digby, 1967; Hardy and Bainbridge, 1951; Knight-Jones and Qasim, 1965; Morgan, 1972). To date, pressure sensitivity among adult brachyurans has been demonstrated only in the portunid crabs *Macropipus holsatus* (Morgan, 1967) and *Carcinus maenas* (Naylor and Atkinson, 1972). In both cases, increased pressure stimulated locomotor activity and the threshold of detection was less than 0.1 atm (or 1 m of water). Since the maximum pressure change induced by the trapezoidal tank was equivalent to only 16 cm of water, it is clear that the corresponding simulated slope of 12° over the length of the tank is substantially less than what true swimming crabs could detect without gravitational cues.

The remaining gradient cue to consider is the substrate slope. At the time these experiments were conducted, we had no feasible means of isolating substrate incline without producing pressure gradient at the same time. However, positive pressure inside a sealed container exerts itself equally and undiminished on all sides (Pascal's Principle). Thus, a crab inside a pressurized rectangular tank, mounted on an incline, will experience a substrate slope in the absence of any pressure gradients. Although this experiment was not conducted, these crabs are morphologically capable of detecting gravitational cues associated with the substrate slope. Typical brachyuran statocysts are located at the bases of the crabs' antennules (Schone, 1971). In addition, their limb proprioceptors can monitor the movement, stress, and position of their ambulatories (Cohen and Dijkgraaf, 1961). This evidence, coupled with the fact that all gradient cues other than substrate slope have been experimentally excluded, leads us to believe that the aspect of gradient to which *Uca pugilator* responds is the gravitational cue that is associated with substrate slope.

Generalizations cannot be made concerning the behavioral differences between Florida and Long Island crabs since the samples tested were only from two beaches. Further testing on other Gulf and Atlantic coast beaches would be needed to detect any true differences in the proportions of shoreward orienting crabs, or any clines of orientation time. Potential differences might be due to the genetic composition of local populations or to environmental factors such as local pollution levels (J. Lincer, Mote Marine Laboratory, personal communication).

Uca pugilator has the ability to orient both on land and underwater. The terrestrial and underwater systems are similar in that they employ redundant schemes of cues, with celestial cues dominating. By inference, this study has shown that, in addition, substrate slope may be used for directional guidance underwater. Its role in above-water orientation, however, has yet to be demonstrated.

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Summary

The semi-terrestrial sand fiddler crab, *Uca pugilator,* occasionally is forced by avian and mammalian predators to go into the water where it becomes vulnerable to aquatic predators. Therefore, it would be adaptive for *Uca* to possess some means of detecting the direction of the shore and its burrow while submerged. Using crabs from Florida and Long Island, New York, the identity of the cues used in underwater orientation and the possible hierarchial arrangement of these cues were ascertained.

Under various cue regimes, the crabs were individually observed in a long narrow tank that allowed the crabs to proceed either toward shore or away from it. The potential cues for shoreward orientation which were available to the submerged crab were celestial cues, landmarks, and gradient cues (hydrostatic pressure, light wavelength, light intensity and substrate slope). Each cue was isolated and then tested for its effectiveness in orientation. It was next presented to the crabs in a conflicting configuration with other cues to determine its relative effectiveness.

The crabs oriented toward shore when presented with either celestial cues, landmarks, or gradient cues. Celestial cues dominated both landmarks and gradient cues, while no clear dominance was observed between landmarks and gradient cues. Gradients of hydrostatic pressure, light wavelength, and/or light intensity were found to be ineffective cues for orientation. This suggests that the gradient cue used for shoreward orientation is the substrate slope. The behavioral differences between Florida and Long Island crabs were also examined.

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